8-1990

Early Life-History Implications of Selected Carcharhinoid and Lamnoid Sharks of the Northwest Atlantic

Steven Branstetter

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Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries

Harold L. Pratt, Jr.
Samuel H. Gruber
Toru Taniuchi (editors)
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64. Illustrated key to penaeid shrimp of commerce in the Americas, by Isabel Pérez Farfan. April 1988, 52 p.


Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries

Proceedings of the Second United States-Japan Workshop
East-West Center, Honolulu, Hawaii
9–14 December 1987

Harold L. Pratt, Jr.
Samuel H. Gruber
Toru Taniuchi (editors)

Sponsored by:
The American Elasmobranch Society,
the Japanese Group for Elasmobranch Studies,
the National Science Foundation, and
Japan Society for the Promotion of Science

August 1990
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WORKSHOP PARTICIPANTS  517
This report owes its genesis to the foresight and enthusiasm of Dr. Kazuhiro Mizue. By happy circumstance, Professor Mizue contacted me in 1983 with his visionary ideas on cooperative programs. He noted that the time was right because the Japan Society for the Promotion of Science and the National Science Foundation had mutually given priority to cooperative programs in marine biology.

I therefore agreed to act as the U.S. coordinator and proposed to NSF, a short trip to Japan to negotiate site visits and timing with ten previously appointed Japanese scientists and, if that trip were successful, to negotiate a joint research project, possibly followed by a joint seminar.

The success of that trip and subsequent funding of the joint seminar and project were due in large part to coordination by my wife Mariko, who speaks Japanese and who made the many office hours of difficult meetings bearable; to Dr. Toru Taniuchi, who kept up a stream of useful information, both social and administrative; and to Dr. Charles Wallace of NSF, who encouraged me from the beginning. Mention should also be given to Dr. Charles Owen of the U.S. Embassy in Tokyo, who helped us through the considerable red tape of international programs in the host country.

After a productive first meeting, during which most of the 13 U.S. and Japanese scientists presented their results at the Second Indo-Pacific Fish Conference in Uyeno, Tokyo, it was decided that we should proceed with a comprehensive joint seminar on chondrichthyan fishery biology. By then, Professor Mizue had retired and Dr. Mikio Oguri became the Japanese principal investigator.

The smooth, efficient staging of four days of meetings was due in large part to James McMahon and his competent staff at the University of Hawaii’s East-West center. We are all in their debt. Finally, this book would have been only an academician’s dream without the efforts of the senior editor who took on the real task of completing it and making it a reality. Thanks Wes!

Samuel H. Gruber
Miami, September 21, 1989
INTRODUCTION

Elasmobranchs have always been important to people dependent on or interested in the sea. They have provided a vast number of products, ranging from food and pharmaceuticals to clothing and novelties. People are fascinated by them. General knowledge and sometimes misinformation about the more dramatic species: stingrays, white and hammerhead sharks, manta rays, and makos, have thrilled and entertained millions of people worldwide.

Studies of their anatomy and systematics have enriched our understanding of other chordate classes, medical science, and the order and structure of taxonomy. Investigations of their ecology and life history help us to understand large marine ecosystems and food webs.

Recently, national interest in shark food products has increased dramatically and a global market has developed. Shark damage to the highly valuable finfish catch is a large financial burden to some countries; consequently many sharks are destroyed. Untold thousands are destroyed as bycatch simply because their economic value is too low for fishermen to keep them. As a result of this multifaceted exploitation and mankind's effects on the environment, elasmobranch stocks are heavily impacted. Conservation and management have not kept pace with utilization. Our knowledge of these important and exciting animals is, and always has been, limited.

The focus of the U.S.-Japan workshop was to address recent advances in elasmobranch research in the hope of providing at least a temporary benchmark and reference work for ourselves, for fellow researchers, for those charged with managing marine resources, and for students of elasmobranch biology. The workshop provided a forum for exchange of ideas and ideologies; and provided both a place at which past joint research projects could be culminated and a point of intersection for new cooperative endeavors.

Fifty-two participants from seven different countries delivered research reports and participated in two workshop sessions. Of the 43 oral papers, 36 were accepted as final manuscripts. Each manuscript was sent to two or three anonymous reviewers. Over 90 reviews were performed by 27 workshop attendees and 39 outside specialists. Japanese and Mexican papers were submitted in English and edited for style, checked by the authors, sent out for peer review with the rest, edited, revised, edited again and double checked by each author.

Manuscripts range in scope from current updates on fisheries landings and trends, both worldwide and local; to evaluations of the unique internal ecology of bacteria in shark tissues. Papers include submersible observations of deep sea sharks and anatomical observations with the superwide field scanning electron microscope. We have tried to create a book that will be worthwhile reading as well as a reference work for many years to come.


I would like to thank my co-editors for comments, help and encouragement as the project proceeded: Jack Casey and Ken Sherman for support and advice; Laura Hedrick for her patience and skill in typing and retyping many of the manuscripts, tables, and correspondence; and Steve Branstetter for transcription of the Workshop audiotapes and help over some rough spots. I thank Frank Murra and Mark Nichols of Sea World, Orlando, for cover art work and Rolf Williams for his hard work on our behalf. My sincere appreciation goes to the reviewers whose quiet work substantially changed and improved the manuscripts. I especially thank all of the authors for sharing their research with us. Together you have carried the lamp of knowledge a little closer toward understanding elasmobranch biology.

Harold L. Pratt, Jr., Senior Editor
Narragansett, October 7, 1989
Early Life-History Implications of Selected Carcharhinoid and Lamnoid Sharks of the Northwest Atlantic

STEVEN BRANSTETTER
Virginia Institute of Marine Sciences
Gloucester Point, VA 23062

ABSTRACT

The size of most newborn sharks makes them susceptible to predation from their own kind and other large fishes. In the northwestern Atlantic, juvenile nursery grounds can be generally classified according to whether or not the young are exposed to such predatory risk. Several related factors—breeding frequency, litter size, size at birth, early growth rate—may help offset early natural mortality. These factors are counterbalanced by the different species in several different ways, producing numerous early life history strategies. In general, slow growing species are either born at relatively large sizes or use protected nursery grounds, whereas faster growing species tend to rely more on growth rates than the other factors.

Introduction

An expanding U.S. recreational (Casey and Hoey 1985) and commercial (Anderson 1985) fishery for sharks in the northwestern Atlantic may be exceeding the estimated maximum sustainable yield (National Oceanic and Atmospheric Administration 1978; Gulf of Mexico Fishery Management Council 1980). Additionally, a long established fishery in Cuba (Anderson 1985) and a strong and growing shark fishery in Mexico (Bonfil et al. 1990) targets the same stock. Management of this stock may soon be necessary which will require detailed life-history information for estimations of stock potential.

Because of the data needed in life-history studies, research often focuses on the adult portions of the stock for information (i.e., reproduction and maturation). Hoening and Gruber (1990) point out that a successful life-history strategy is one where the offspring survive to play another round in the “game of life”; unfortunately, little attention is sometimes paid to the early life-history of most species, although this may be a critical period for certain characteristics—recruitment, survival, and mortality (Hoff and Musick 1990).

For sharks, a successful strategy has been attained by the counterbalancing of several interrelated factors—reproductive frequency, size at birth, litter size, growth rate, and the use of nursery areas (Fig. 1). Viviparous sharks, in general, are K strategists (Planka 1971; Holden 1977). They are relatively long-lived and slow growing with reproductive energy expended in the production of a relatively small number of precocious young after a lengthy gestation period (see Cailliet et al. 1986; Cailliet 1990 for a review). Viviparity restricts fecundity, thus there is a direct relationship between the number and/or size of the young produced and the size of the mother. For several carcharhinid species, the smaller (younger) the mother, the fewer the number of offspring produced per litter (Bass et al. 1973; Parsons 1983b; S. Branstetter, unpubl. data). Additionally, the inverse relationship between number and size of embryos per litter documented for the Atlantic sharpnose shark, Rhizoprionodon terraenovae (Parsons 1983b), should be expected for most viviparous species. Given the limited space available to carry young, a female can produce either a large number of small young, or a small number of large young.

Shark pups are precocious, and cohort survival may be dependent on an early life history that allows for attainment of a certain minimum size which both deters predators and increases swimming efficiency and speed (Thompson and Simaneck 1977; Webb and Keyes 1982) so that the individual can actively avoid predation. It is unlikely that food is a major limiting factor to their survival, considering that the young usually occupy estuarine or coastal habitats that are also occupied by numerous fish and invertebrate species which serve as available prey items for these opportunistic feeders. Young sandbar sharks are able to selectively feed on specific prey items (Medved and Marshall 1981; Medved et al. 1985, 1988). Additionally, based on the high oil content in the livers of immature sharks, Springer (1967) postulated that they have little difficulty finding sufficient food. Thus predation may be the most important source of mortality on the young sharks.
Predatory risk to the young may be greatest from other sharks, especially adult sharks, and other large fishes such as groupers (Randall 1977) may also be a source of natural mortality. Small sharks, either young sharks or adults of small species, are frequently recorded as food items of larger sharks (Castro 1983). Usually, greater than 50% of shark stomachs are empty upon examination, even when collected by passive (nonattracting) methods such as gill nets (Bass et al. 1973; Snelson et al. 1984; Killam 1987). Few detailed quantitative food habits studies exist (Medved and Marshall 1981; Stillwell and Kohler 1982; Medved et al. 1985, 1988); stomach contents are usually listed qualitatively (Clark and von Schmidt 1965; Sadowsky 1967; Branstetter 1981). However, frequency of occurrence of shark remains is often 10–15% in those stomachs containing food, especially for certain species such as Carcharhinus obscurus, C. leucas, and Galeocerdo cuvieri (see Bass et al. 1973 for an excellent summary).

Additionally, the smaller the shark, the more vulnerable it is to such predatory risk. Off Brazil, the most common sharks noted in the stomach contents of seven species of sharks were neonatal or young Carcharhinus porosus, Sphyrna lewini, S. tiburo, and young and adult Rhizoprionodon porosus, and R. lalandei; even adults of the intermediate sized C. porosus ($L_{\text{max}}$ $\sim$140 cm) fed on neonatal S. lewini and R. lalandei (Sadowsky 1967). All of these prey species are relatively small sharks.

One of the important predatory shark species is the bull shark, Carcharhinus leucas, which has been reported to feed on small C. limbatus, C. acronotus, C. isodon, C. plumbeus, and C. porosus (Springer 1960, 1963, 1967; Tuma 1976; Sadowsky 1967, 1971; Snelson et al. 1984). Springer (1960) suggested the bull shark was a major source of mortality on young sandbar sharks, C. plumbeus, and Sadowsky (1971) noted that even young (adolescent?) bull sharks preyed on small sharks, including neonatal Sphyrna tiburo.

Such predatory risk is reduced for many species by the use of nursery grounds for the young. These nursery grounds serve a two-fold purpose: by segregating the young from the adult populations they offer protection from predation and they usually have numerous prey items for the pups. The nursery grounds can be categorized by their degree of exposure to potential predators. Some are "protected," because they are in areas infrequently inhabited by adult sharks, while others are very "unprotected," because they are located in habitats occupied by adults.

Additionally, the speed at which maturity is attained may also contribute to cohort strength and recruitment. Small species, such as Rhizoprionodon terraenovae, mature more quickly and reproduce more often than larger species such as the bull shark, Carcharhinus leucas (Parsons 1985; Branstetter 1987a, Branstetter and Stiles 1987).

Hoenig and Gruber (1990) discuss the importance of several biological parameters related to management purposes. Data are now available for many of these characteristics (see Pratt 1990 and Cailliet 1990 for a review), and based on such data, I have categorized the species into groups with similar life-history characteristics (Table 1). Given the restrictions of viviparity as outlined earlier, a female can produce either a few, large young, or numerous, small young. For the shark species considered here, both options occur: the production of relatively few young (<15; usually 6–8) that, at birth, are >20% of the maximum adult size ($L_{\text{max}}$) (total lengths are used throughout this report), or the production of more numerous young (30–70) at <20% $L_{\text{max}}$. It should be pointed out that these are minimal values as most adults are smaller than $L_{\text{max}}$; the average female Rhizoprionodon terraenovae is $\sim$95 cm, with $L_{\text{max}}$ = 110 cm. These two groups must be further subdivided by the actual size of the pups because size terminology here is relative. For example, the small ($L_{\text{max}}$ 110 cm) Atlantic sharpnose shark produces pups that are 30–35 cm at birth. This is a large pup compared to the mother (∼30% $L_{\text{max}}$), but small compared to the size at birth for larger species or to potential predators. For this discussion, I have distinguished two categories: small pups (<70 cm at birth) and large pups (>70 cm at birth).

Growth data are now available for many species. For this discussion, growth rates are categorized by the Brody growth coefficient $K$ (Ricker 1975) and have been separated at the value of < or > 0.10. Several species have estimated $K$ values of >0.20; with future data on additional species, further subdivisions might be beneficial. However, $K$ values, although providing a comparative constant for overall life history, may not adequately represent early
Table 1.
Species groups of selected carcharhinoid and lamnoid sharks of the northwestern Atlantic based on life history characteristics. Lengths and growth expressed as cm TL. BL = birth length. $K$ represents the Brody growth coefficient. See citations in the text for data sources for each species.

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<th>$L_{max}$</th>
<th>Birthsize (% $L_{max}$)</th>
<th>No. young</th>
<th>Yr. 1 growth (% BL)</th>
<th>$K$</th>
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<tr>
<td>Small young</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. leucas</td>
<td>300</td>
<td>70(23%)</td>
<td>6-10</td>
<td>15(22%)</td>
<td>0.07</td>
</tr>
<tr>
<td>C. plumbeus</td>
<td>250</td>
<td>65(26%)</td>
<td>6-10</td>
<td>15(23%)</td>
<td>0.05</td>
</tr>
<tr>
<td>N. brevirostris</td>
<td>300</td>
<td>65(22%)</td>
<td>6-18</td>
<td>15(23%)</td>
<td>0.05</td>
</tr>
<tr>
<td>Large young</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>O. taurus</td>
<td>300 +</td>
<td>100 + (33%)</td>
<td>2</td>
<td>30(30%)</td>
<td>0.07-0.09</td>
</tr>
<tr>
<td>Small young</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. longimanus</td>
<td>275 +</td>
<td>65(24%)</td>
<td>10-15</td>
<td>20(30%)</td>
<td>0.04-0.09</td>
</tr>
<tr>
<td>Large young</td>
<td></td>
<td></td>
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<tr>
<td>C. obscurus</td>
<td>360</td>
<td>90(25%)</td>
<td>10-12</td>
<td>15(16%)</td>
<td>0.07</td>
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<td>C. carcharias</td>
<td>650</td>
<td>140(22%)</td>
<td>8-10</td>
<td>40(30%)</td>
<td>0.06</td>
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<td>Coastal</td>
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<tr>
<td>R. tarmacoenae</td>
<td>110</td>
<td>32(29%)</td>
<td>6-8</td>
<td>22(69%)</td>
<td>0.35-0.50</td>
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<tr>
<td>S. tiburo</td>
<td>120</td>
<td>30(25%)</td>
<td>6-8</td>
<td>20(67%)</td>
<td>0.34-0.58</td>
</tr>
<tr>
<td>C. pororus</td>
<td>134</td>
<td>30(22%)</td>
<td>6</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>C. isodon</td>
<td>160</td>
<td>50(31%)</td>
<td>6-8</td>
<td>25(50%)</td>
<td>0.10-0.22</td>
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<tr>
<td>C. arcenotus</td>
<td>165</td>
<td>45(27%)</td>
<td>4-6</td>
<td>17(38%)</td>
<td>0.13</td>
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<tr>
<td>C. limbatus</td>
<td>200</td>
<td>55(27%)</td>
<td>6-10</td>
<td>35(65%)</td>
<td>0.20-0.27</td>
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<tr>
<td>C. brevipinnia</td>
<td>240</td>
<td>65(27%)</td>
<td>6-10</td>
<td>40(62%)</td>
<td>0.22</td>
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<th>Species</th>
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<th>No. young</th>
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<td>Pelagic</td>
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<td></td>
</tr>
<tr>
<td>C. signatus</td>
<td>275 +</td>
<td>65(26%)</td>
<td>10-18</td>
<td>32(50%)</td>
<td>0.10-0.15</td>
</tr>
<tr>
<td>C. falciformis</td>
<td>310</td>
<td>70(23%)</td>
<td>10-15</td>
<td>45(65%)</td>
<td>0.15</td>
</tr>
<tr>
<td>L. narinus</td>
<td>270</td>
<td>70(25%)</td>
<td>2</td>
<td>33(45%)</td>
<td>0.11</td>
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<tr>
<td>I. oxyrinchus</td>
<td>375</td>
<td>70(20%)</td>
<td>8-10</td>
<td>40(57%)</td>
<td>0.20-0.27</td>
</tr>
<tr>
<td>A. supercilios</td>
<td>400</td>
<td>100(25%)</td>
<td>2</td>
<td>40(36%)</td>
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? ← C. perezi
C. brachyurus → ?
? ← C. altimus
? ← C. galapagensis

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<th>Species</th>
<th>$L_{max}$</th>
<th>Birthsize (% $L_{max}$)</th>
<th>No. young</th>
<th>Yr. 1 growth (% BL)</th>
<th>$K$</th>
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<tr>
<td>S. mokaram</td>
<td>560</td>
<td>70(13%)</td>
<td>30-40</td>
<td>?</td>
<td>?</td>
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<tr>
<td>S. lewini</td>
<td>310</td>
<td>45(15%)</td>
<td>30-40</td>
<td>17(38%)</td>
<td>0.07</td>
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<td>Small young</td>
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<tr>
<td>S. zygaena</td>
<td>390</td>
<td>50(13%)</td>
<td>20-40</td>
<td>?</td>
<td>?</td>
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<tr>
<td>Large young</td>
<td></td>
<td></td>
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<tr>
<td>C. carcharias</td>
<td>760</td>
<td>140(18%)</td>
<td>8-10</td>
<td>40(30%)</td>
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<th>$K$</th>
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<td>G. caviari</td>
<td>450</td>
<td>70(16%)</td>
<td>30-70</td>
<td>70(100%)</td>
<td>0.11-0.18</td>
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<th>Species</th>
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<th>Birthsize (% $L_{max}$)</th>
<th>No. young</th>
<th>Yr. 1 growth (% BL)</th>
<th>$K$</th>
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<td>P. glaucia</td>
<td>350</td>
<td>45(13%)</td>
<td>40-80</td>
<td>40(90%)</td>
<td>0.11-0.25</td>
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</table>

growth and attainment of minimum sizes as considered in this discussion. Therefore, early growth is also discussed as a ratio of the first year’s growth compared to the length at birth (BL). As an example, the Atlantic sharpnose shark is born at ~32 cm and increases ~22 cm in length during its first year (Parsons 1985; Branstetter 1987a), for a first years’ growth of 69% BL. This is rapid growth, but the shark is still relatively small compared to potential predators. A one year old sharpnose shark is still smaller than a neonatal Carcharhinus limbatus.

Several important characteristics such as recruitment and survival/mortality, especially in relation to their early life history, are still poorly understood (Hoff and Musick 1990). Although it is probably impossible, at present, to make
accurate estimates of these parameters, this paper attempts to draw on the known characters to make some inferences about the early life history of species that may help answer some of the remaining questions.

Species with Slow Growth
\(K < 0.1; < 30\% \text{ BL}

This group is divided according to the size of the newborns and the kind of nursery grounds they use: 1) exceptionally large (\(\approx 100 \text{ cm}\)) young that occupy coastal and surf areas that expose them to predators, or 2) smaller (\(< 70 \text{ cm}\)) young that use bays and estuarine areas as nursery grounds, thus avoiding potential predators. This group can be further subdivided by the relative size of the young compared to the adults (see Table 1), but the two primary categories are adequate for this discussion.

Species with Large Neonates

The sand tiger, Odontaspis taurus, is a common, large coastal shark of warm-temperate regions, reaching a maximum size of \(> 300 \text{ cm}\) (Springer 1960; Gilmore et al. 1983). The embryos are oviparous and cannibalistic during development; therefore, only two extremely large (\(> 100 \text{ cm}\)) young (Gilmore et al. 1983) are generally produced. Nursery grounds are littoral, temperate waters, but do not include embayments or low salinity areas (Bass et al. 1975b); thus, the young are exposed to predation by the abundant adult sharks of these areas. Age and growth data are lacking for this species except for captive specimens discussed in Gilmore et al. (1983), but using their length at age data in Ford/Walford plots (Ricker 1975) I calculated a \(K\) value of \(0.07-0.09\). First year growth was \(\approx 30\% \text{ BL}\) under these optimal environmental conditions. Even if the actual growth rate is slower, first year growth coupled with the initial large size of the pups should decrease predatory risks on the young.

Similarly, the dusky shark, Carcharhinus obscurus, a large \((L_{\text{max}} \approx 360 \text{ cm})\) Garrick 1982 common shark of continental shelf and insular regions, gives birth to young at a relatively large size (80-100 cm) (Clark and von Schmidt 1965; Bass et al. 1973; Branstetter 1981; Compagno 1984). Nursery grounds appear to be surf zone areas, but do not include embayments or lowered salinity areas (Bass et al. 1973). As with Odontaspis taurus, the large size of neonates may reduce predation by the adults of the common coastal sharks. However, the 10-15 young produced in each litter (Clark and von Schmidt 1965; Dodrill 1977; Branstetter 1981) suggest that mortality rates on these young may be high. Bass et al. (1973) listed C. obscurus pups as a food item of C. limbatus, and O. taurus is also known to prey on the C. obscurus pups (J. Musick, Virginia Inst. Mar. Sci., Gloucester Point, VA, 23062, pers. comm., 1988). The pups grow slowly, only about 15 cm/yr (16% BL; \(K = 0.07\), calculated from data of Schwartz 1983), but the pups would be \(> 100 \text{ cm}\) by one year of age. Again, attainment of this size may reduce mortality rates.

A third variation of this pattern is exemplified by the white shark, Carcharodon carcharias. This species is known to attain a length of 600 cm, and is estimated to reach a maximum size of \(> 760 \text{ cm}\) (Cailliet et al. 1985). Unlike most lamnoids which produce 2-4 young, the white shark produces 8-10 young per litter (Randall 1973; S. Uchida, Okinawa Aquarium, Okinawa, Japan, pers. comm., Dec. 1987), at approximately 140 cm (Stevens 1984; Cailliet et al. 1985). Although these are large pups, they are small compared to the adults (approximately 18% \(L_{\text{max}}\)). Based on the capture localities of young (Cailliet et al. 1985; Casey and Pratt 1985), birth probably occurs in neritic or pelagic cool temperate waters. The pups grow \(\approx 30\% \text{ BL}\) (\(K = 0.06\); Cailliet et al. 1985; Welden et al. 1987) their first year, and would be larger than most potential predators. Randall (1987) presented evidence refuting several length records of the white shark (\(> 460 \text{ cm}\)). Should their maximum size be near 650 cm instead of the 760 cm estimated by Cailliet et al. (1985), they would need to be categorized in Table 1 with Carcharhinus obscurus (birth \(> 20\% L_{\text{max}}, K < 0.1, < 30\% \text{ BL}\)).

Species with Small Neonates

Three species in this group have very similar patterns. The bull shark, Carcharhinus leucas, and the sandbar shark, C. plumbeus, are common in warm temperate coastal waters, and the lemon shark, Negaprion brevirostris, is more common in tropical environments. C. leucas reaches a maximum size of \(\approx 300 \text{ cm}\) (Sadowsky 1971; Garrick 1982; Branstetter and Stiles 1987). C. plumbeus a maximum size near 250 cm (Springer 1960; Casey et al. 1985), and both produce 6-10 young 60-70 cm in length (Springer 1960; Clark and von Schmidt 1965; Branstetter and Stiles 1987), although some C. leucas pups develop to extraordinary size (75-85 cm) at the expense of their intra-uterine litter mates (Sadowsky 1971; Dodrill 1977; Branstetter and Stiles 1987).

Both C. leucas and C. plumbeus pups grow slowly (C. leucas—\(K = 0.07\); Thorson and Lacy 1982; Branstetter and Stiles 1987; C. plumbeus—\(K = 0.05\); Casey et al. 1985), increasing in length approximately 15 cm/yr (22% BL for C. leucas, 23% BL for C. plumbeus). C. leucas uses bays and estuaries of the Gulf of Mexico and the east coast of Florida as nurseries and the pups penetrate freshwater areas (Caillouet et al. 1969; Dodrill 1977; Branstetter 1981; Snelson and Williams 1981; Snelson et al. 1984) as they do in other parts of their range (Bass et al. 1973; Thorson and Lacy 1982). C. plumbeus pups occupy the lower portions of bays and sounds (Branstetter 1981; Casey et al. 1985).

Both species frequent estuaries for several years. In the fall of their first year, the pups are \(\approx 85 \text{ cm}\) (Snelson et al.
1984; Casey et al. 1985), and they move offshore to overwinter at the continental shelf edge (Springer 1960; Branstetter 1986). They return again to the bays the next spring; juveniles of a size corresponding to one-year-old sharks are common in estuarine areas (Caillouet et al. 1969; Sadowsky 1971; Branstetter 1981; Casey et al. 1985). At lengths of ~120 cm for *C. plumbeus* and 130 cm for *C. leucas* (Sadowsky 1971; Casey et al. 1985; Branstetter and Stiles 1987) both species begin occupying primarily continental shelf waters. At this length they are large enough to avoid predation because of both their size and speed.

In warm temperate regions, *Negaprion brevirostris* has a similar early life history to the bull and sandbar sharks, however the species is not as common in these regions. More commonly found in tropical regions, this large shark (*L*$_{\text{max}}$ 300 cm: Springer 1950a, 1960; Clark and von Schmidt 1965) gives birth to pups 60–70 cm in length. The pups occupy shallow coral reef flats as a nursery ground (Clark and von Schmidt 1965; Gruber 1981, 1982; Gruber and Stout 1983), and grow ~15 cm/yr (20–25% BL) (*K* = 0.05 following data of Gruber and Stout 1983). The shallow reef flats offer protection for these juveniles, although predation by adults of their own species and other large sharks may result in a 50% mortality rate (S. Gruber, RSMAS, Univ. Miami, 31419, pers. commun., June 1987). Litters of 8–18 (*x* = 12) pups (Clark and von Schmidt 1965) may help offset this mortality rate.

The protected nursery area strategy is varied slightly by the scalloped hammerhead, *Sphyrna lewini*. This species attains a length >300 cm and, as an adult, occupies offshore waters more commonly than coastal waters (Clarke 1971; Klimley 1981; Branstetter 1987b). The species produces numerous small young (>30/litter) at 40–50 cm, which occupy bays, sounds, and beach front areas as a nursery (Sadowsky 1965; Clarke 1971; Bass et al. 1975a; Dodrill 1977; Snelson and Williams 1981; Branstetter 1987b). These young grow ~15 cm in the first six months, and 15 cm/yr for the next two years (*K* = 0.07; Schwartz 1983; Branstetter 1987b). (This growth rate is 38% BL, which is a larger value than the category in which they are placed (<30% BL), but it is still much slower than most of the rapid-growing species with growth rates >50% BL). Instead of remaining in the protected nurseries, the pups move into littoral regions after the first three months where they are exposed to predation (Sadowsky 1967; Clarke 1971; Snelson and Williams 1981; Branstetter 1987b).

*Sphyrna lewini* pups were the most common shark in stomach contents listed by Sadowsky (1967), and Clarke (1971) noted they were preyed upon heavily by adult males of their own species in Hawaii. This apparent high mortality rate among cohorts may be compensated for by the large litter size.

Similarly, the oceanic whitetip shark, *Carcharhinus longimanus* (*L*$_{\text{max}}$ 270–300 cm: Bass et al. 1973) is an offshore species that gives birth to relatively large litters (12–16 pups) at a small size, about 65 cm (Backus et al. 1956; Garrick 1982; Stevens 1984). Limited age/length data (Saika and Yoshimura 1983) suggest this species grows slowly; juvenile growth is about 20 cm/yr (30% BL) (*K* = 0.04–0.09: from data in Saika and Yoshimura 1985), therefore the pups, born in oceanic tropical waters, are more vulnerable to predation, except that few species occupy such water, although those that do are relatively abundant. Attainment of a size that would deter predation may require two to three years. The larger litter size may offset this longer vulnerability to such predatory risk.

The overall biology of the great hammerhead, *Sphyrna mokarran*, and the smooth hammerhead, *S. zygaena*, are poorly understood. However, available data (Clark and von Schmidt 1965; Sadowsky 1965, 1971; Bass et al. 1975a; Castro 1983; Stevens 1984) indicate their life histories are similar to that of *S. lewini*, and for the time being, they are included in this group. They both produce large numbers of young (20–40) after approximately a one-year gestation period. *S. mokarran* pups are born at 70 cm (13% *L*$_{\text{max}}$), and are taken along beach areas (Dodrill 1977; Branstetter, unpubl. data). Growth may be similar to that of *S. lewini* (Branstetter, unpubl. data). Little is known of the biology of *S. zygaena*; pups are born at ~50 cm (13% *L*$_{\text{max}}$) and may occupy a more oceanic zone.

**Species with Fast Growth**

(*K* > 0.1; >40% BL)

This category contains the majority of species under consideration in this review. It also contains a wide range of sharks; small sharks that reach a maximum size of approximately 100 cm to large species that attain in excess of 300 cm maximum length. Nursery grounds for the pups of these species tend to be exposed to predators to varying degrees. Cohort survival appears to be more dependent on cohort strength and growth rate than on occupation of a protected nursery ground. As with slow-growing species, attainment of a size that both deters predation and increases swimming efficiency appears to be an important survival factor. The species in this group can be divided between coastal and pelagic species with the coastal group further subdivided by the size attained by the species.

**Small (*L*$_{\text{max}}$ ~100 cm) Coastal Sharks**

This group includes the sharpnose sharks, *Rhizoprionodon* spp., the bonnethead, *Sphyrna tiburo*, the smalltail shark, *Carcharhinus porosus*, and certain traits of this group are applicable to intermediate-sized species such as the finetooth shark, *C. isodon*, and the blacknose shark, *C. acronotus*. The well studied Atlantic sharpnose shark, *R. terraenovae*, (Parsons 1983a, 1983b, 1985; Branstetter 1981, 1987a) is a good example of the strategy followed by this group. The species
occurs in warm temperate waters of the southeastern United States and is the most common shark taken in the Gulf of Mexico (Cody et al. 1981; Branstetter 1981, 1986). This small shark (<110 cm) is probably vulnerable to predation throughout its life history. Adult R. porosus and R. lalandei are common food items of larger sharks (Sadowsky 1982). It grows comparatively fast (69% BL) \((K = 0.35-0.50): \) Parsons 1985; Branstetter 1987a) with males reaching maturity in three years, females in four years. In areas where reproduction occurs, catch rates for females outnumber males in the adult population 3:1 (Branstetter 1981; Parsons 1983b). Females give birth to 4–6 young annually; there is no resting stage in the female reproductive cycle as is common in larger carcharhinids (Pratt 1979; Branstetter 1981; Parsons 1983b). The pups, although small at birth (30–33 cm), are large compared to the size of the mother (29% of \(L_{\text{max}}\)). Nursery grounds are littoral zones, including beach and surf areas. The young also occur in the mouths of bays and coastal sounds, possibly migrating with tidal fluctuations (Parsons 1983b; Branstetter 1986, 1987a). Adults of several shark species occupy these littoral zones, and mortality of newborns should be significant. In other areas neonatal R. porosus and R. lalandei are common food of larger sharks (Sadowsky 1967). Adequate adult recruitment may be dependent on large annual cohorts and rapid maturation. This is suggested by 1) the possible domination of females in reproductively active populations, 2) an annual reproductive cycle without a resting stage, and 3) the production of numerous young as large as can be accommodated in the female body cavity. Parsons (1983b) suggested that females that produce fewer, larger young may be the most efficient.

Similarly, the life history of the bonnethead, Sphyrna tiburo, recently described by Parsons (1987) suggests it may suffer from a higher mortality because of its small size. This shark, reaching a maximum length of 120 cm, grows rapidly \((K = 0.34–0.58)\) maturing in about two years, and produces 6–9 young a year. The reproductive cycle is very short, 4–5 months, and the pups are born at 25–33 cm depending on locality and environmental factors. Pup growth is rapid, 20+ cm/yr (67–80% BL). The pups are found in bays and coastal waters, where they are often preyed upon by larger sharks (see Introduction) (Sadowsky 1967).

Little is known about C. porosus. It reaches a maximum size of \(\sim\)140 cm, and produces <10 young per litter. Its size and general habitat preference suggest it is similar to the other species (Garrick 1982; Compagno 1984; J. Castro, Clemson Univ., SC 29631, pers. commun., Nov. 1988).

**Large \((L_{\text{max}} > 150 \text{ cm})\) Coastal Sharks**

Life histories for medium-sized species such as Carcharhinus isodon \((L_{\text{max}} = 160 \text{ cm})\) are described by Springer 1950b; Branstetter and Shipp 1980) and C. acronotus \((L_{\text{max}} = 165 \text{ cm})\) are intermediate between the small species and larger coastal sharks. The female reproductive cycle has a one year resting stage similar to larger sharks, but the young (4–6/litter) are relatively small at birth (45 cm for C. acronotus and 50 cm for C. isodon [Branstetter and Shipp 1980; Branstetter 1981; Schwartz 1984]). They occupy littoral zones where they are exposed to predation from the abundant coastal sharks. Both species grow at a moderate rate; neonates increase approximately 20 cm in their first year (\(\sim\)50% BL for both species) \((C. acronotus\) \(K = 0.13: \) Schwartz 1984; C. isodon \(K = 0.10–0.22\) Branstetter, unpubl. data). Pups of both species are known prey items of the bull shark. As with the smaller sharks, an earlier maturation may help offset mortality rates.

The two common species in the category, the blacktip shark, Carcharhinus limbatis, and the spinner shark, C. brevipinna, have similar life history patterns (Clark and von Schmidt 1965; Branstetter 1981, 1987c). These two species comprise 1/3 to 1/2 of the catch of epipelagic coastal sharks taken on longlines in the Gulf of Mexico (Branstetter 1987c). In the northwestern Atlantic region both species reach a maximum size of >200 cm, with C. brevipinna being the larger of the two, reaching 240 cm. Both produce 6–10 young after a 12 month gestation period in a two-year reproductive cycle. C. limbatis pups are born at 50–60 cm, and C. brevipinna pups are born at 60–70 cm (Branstetter 1981, 1987c). Both use the relatively unprotected littoral zones as nurseries, and pups invade lower portions of bays and sounds with the tide, but neither penetrate low salinity areas (Snelson and Williams 1981; Branstetter 1987c).

Growth for both species is relatively fast: C. limbatis \(K = 0.20–0.27\); C. brevipinna \(K = 0.22\) (Killam 1987; Branstetter 1987c). Pups increase >20 cm in the first six months of life. They apparently continue to grow through the first winter after they move offshore to deep regions of the outer continental shelf. When they return to coastal waters in the spring, they have attained lengths in excess of 90 cm for C. limbatis (85% BL) and 100 cm for C. brevipinna (67% BL). These one-year-old sharks are common in littoral zones. Growth continues at 15–20 cm/yr through the second year, thus they attain a size that may deter predators, and allow them to attain swimming speeds to actively avoid predation.

**Pelagic Species**

Similar to coastal carcharhinids, the silky shark, C. falciformis, apparently depends on rapid growth for adequate neonate survival. In the central Pacific, Strasburg (1958) noted the silky shark was twice as abundant in neritic waters compared to open ocean situations, and in the Gulf of Mexico the species is more common along the edge of the continental shelf (150–500 m) (Branstetter 1987b). This
large (>300 cm) cosmopolitan epipelagic shark gives birth to 6–14 young at 70–75 cm (Strasburg 1958; Bane 1966; Bass et al. 1973; Cadenat and Blache 1981; Branstetter 1987b). In the tropics, this shark may not have a seasonal gestation period (Strasburg 1958; Bane 1966; Stevens 1984), but in the warm-temperate Gulf of Mexico, it appears to give birth in summer (June–August) (Branstetter 1987b). Springer (1967) suggested that neonates inhabit deep reef areas along the continental shelf edge, but apparently they move to a pelagic existence by the first winter (6 months of age) (Branstetter 1987b). Their size at birth makes the pups vulnerable to predation from the large epipelagic sharks of the region. Cohort survival appears to be enhanced by rapid growth (K = 0.15) and schooling behavior (Branstetter 1987b). The pups increase 25–30 cm in length by the first winter, and are approximately 115 cm by 1 year of age (65% BL). Neonates are taken on pelagic longlines during the winter in the Gulf of Mexico (Branstetter 1981, 1987b), separate from the subadult and adult part of the population. Yoshimura and Kawasaki (1985) also noted juvenile silky sharks in the western central Pacific tended to aggregate by size.

Another pelagic carcharinid, the night shark, Carcharhinus signatus, may have a similar early life history. This species occurs in deep waters along the edge of the continental shelf on both sides of the Atlantic and may be most abundant in the Florida Straits (Raschi et al. 1982; Garrick 1985; Branstetter and McEachran 1986a). C. signatus reaches a maximum size near 275 cm, and gives birth to 12–18 pups at 60–70 cm (Branstetter 1981, 1986; Garrick 1985). These pups occupy the epipelagic zone along the continental shelf edge where they are exposed to predators. Accurate age and growth data are lacking for this species, but preliminary data indicate the pups grow 30–35 cm yr (50% BL) (K = 0.10–0.15 following data in Branstetter 1986), attaining a length in excess of 100 cm in a little over a year, similar to that of the silky shark.

The pelagic aloipids and lamnids have similar strategies with the young being dependent on size for survival. Most lamnoids produce 2–4 large (~100 cm) young (Bass et al. 1975b; Gruber and Compagno 1981; Otake and Mizue 1981; Gilmore 1983), but the shortfin mako, Isurus oxyrinchus, (Lmax 375 cm; Pratt and Casey 1983) produces numerous young (6–18) that are comparatively smaller (70 cm) (Gohar and Mazar 1964; Gubanov 1972, 1978; Stevens 1983, 1984; Branstetter 1981, unpubl. data). The size of neonate I. oxyrinchus makes them more vulnerable to predators, but the larger litter size may offset this mortality rate. In the northwest Pacific the population has a relatively fast growth rate with juveniles increasing approximately 40 cm yr (57% BL) for the first two years (K = 0.203–0.266; Pratt and Casey 1983). Such rapid length-increases and associated increased swimming efficiency and speed should reduce predatory risks.

In contrast, the much larger (Lmax >420 cm: Gilmore 1983) longfin mako, I. paucus, a tropical mesopelagic species that rarely enters continental shelf waters (Doddrell and Gilmore 1979; Killam and Parsons 1986) gives birth to two young at >100 cm (Gilmore 1983). As with other offshore pelagic sharks, a nursery ground, per se, may not be used; females probably give birth in open ocean waters, and the pups remain in pelagic waters. The young are of a size that should deter predators and allow them to attain swimming speeds necessary to actively avoid predation (Gilmore 1983). Growth rates are unknown, but Branstetter (1986) reported similar numbers of vertebral bands in similar sized I. oxyrinchus and I. paucus, suggesting they have similar growth rates (40 cm yr); growth through the first year would be near 40% BL.

The porbeagle, Lamna nasus (Lmax 260–280 cm: Aasen 1963), also gives birth to smaller young, similar to Isurus oxyrinchus (~70 cm: Aasen 1963), but produces only two or possibly four per litter. Neonates increase to approximately 100 cm (45% BL) in their first year (K = 0.11: Aasen 1963). Predation risks may not be as great for the young of this species because few large predators exist in the boreal waters that this species inhabits. An estimated mortality (M) for a virgin stock of this species was approximately 0.18 (Aasen 1963), and much of this can probably be attributed to juvenile mortality.

The aloeipids only produce 2–4 young that are of intermediate size at birth. Lengths for this group are difficult to compare because of the exaggerated upper caudal lobe. Although the pups are not large, it is possible that this added size factor could inhibit some predation. The bignose shark, Alopias superciliosus, which reaches a maximum size near 600 cm (225 cm pre-caudal length [PCL]) (Gilmore 1983) produces young born at 100–110 cm (55–60 cm PCL) (Bass et al. 1975b; Gruber 1980; Gruber and Compagno 1981; Gilmore 1983), and thresher shark, A. vulpinus, (Lmax 650 cm [325 cm PCL]; Cailliet et al. 1983) young are slightly larger (115–160 cm [65–90 cm PCL]) (Gubanov 1978; Hixon 1979; Cailliet et al. 1983). The third species, the pelagic thresher, A. pelagicus, which does not occur in the northwest Atlantic, may also be born at ~100 cm (Otake and Mizue 1981). Little is known of the habits of A. superciliosus and A. pelagicus young, but the juveniles are taken on longlines in open ocean pelagic waters. Their size, coupled with a relatively rapid growth rate may be adequate for survival (Gilmore 1983). Gruber and Compagno (1981) estimated growth for newborn A. superciliosus at ~40 cm yr (36% BL). On the basis of their data I calculated a K of 0.3, but Gruber and Compagno warned that their growth estimates were only first order approximations. A. vulpinus is associated more with continental shelf waters, especially the young (Bass et al. 1975b; Gubanov 1978; Branstetter 1981; Cailliet et al. 1983). These waters are occupied by numerous carcharhinid and lamnoid sharks, thus the young are exposed to
greater predatory pressures than their oceanic congeners. Their larger size at birth and rapid juvenile growth \( (K = 0.11-0.21; \) Cailliet et al. 1983; Cailliet and Bedford 1983; Cailliet and Radtke 1987) of 40 cm/yr \( (>25\% \text{ BL}) \) may offset such predation.

**Rapid Growth, Large Litters**

The last two species to be considered here also have rapid growth rates but produce comparatively large numbers of young; this fact suggests that mortality rates on the young may be high compared to other species. The blue shark, *Prionace glauca*, is one of the most common offshore pelagic sharks of temperate and tropical waters (Strasburg 1958; Stevens 1984), reaching a size of at least 350 cm (Pratt 1979; Cailliet and Bedford 1983; Compagno 1984). *P. glauca* gives birth to numerous (40–80), small (40–50 cm) young in epipelagic oceanic waters (Pratt 1979; Stevens 1984), similar to the lamnoids. However, their small size suggests they are vulnerable to predation. Little is known of blue shark early life history, but growth studies for the Atlantic population \( (K = 0.13; \) Aasen 1966; \( K = 0.11; \) Stevens 1975, 1976) and the Pacific population \( (K = 0.17-0.25; \) Cailliet et al. 1983; Cailliet and Bedford 1983) indicate neonates nearly double in length (40 cm/yr) their first year (90% BL). During the second year they grow approximately 30 cm, with growth gradually decreasing through maturity. Even with a rapid growth rate, mortality may be high on young cohorts as suggested by the litter size.

The tiger shark, *Galeocerdo cuvieri*, also grows extremely fast in early life \( (K = 0.11-0.18; \) Branstetter et al. 1987). This species, reaching a maximum length of 400–450 cm, gives birth to numerous (40–70) young that are small (70 cm) compared to the adults (Kauffman 1950; Bass et al. 1975a; Branstetter 1981; Branstetter et al. 1987). Specific nursery areas are unknown, but the young are born in coastal waters that expose them to predation by the abundant coastal species, including their own. At birth, they are extremely long and slender and produce an inefficient anguilliform-type swimming motion, and the caudal fin has a low thrust angle (Thompson and Simanek 1977), thus precluding a rapid swimming speed. Neonates grow rapidly, doubling in length the first year of life (100% BL) to ~140 cm (Clark and von Schmidt 1965; Branstetter et al. 1987). Rapid linear growth (30 cm/yr) continues for the next two years until the sharks exceed 200 cm in length. Throughout this period they remain relatively slender-bodied, but swimming efficiency may increase through increased body rigidity and increased caudal fin thrust angle. At 200 cm, linear growth begins to decline, and the rate of weight gain increases, but by this time, they are larger than most potential predators and probably are predators on younger sharks themselves.

**Conclusions**

Shark species vary several life-history characteristics to provide for adequate cohort survival. The attainment of approximately 100 cm TL may be a critical factor in neonate survival as they are then large enough to deter many predators as well as active enough to avoid predation by means of increased swimming speed and efficiency. This may be accomplished by two different strategies: 1) rapid growth in nursery grounds exposed to predators, or 2) slow growth in protected nursery grounds. Small species which are nearing their maximum size at 100 cm are probably susceptible to predation throughout their life history and offset this higher mortality rate with a higher fecundity.

From the categories in Table 1, 14 of the 26 species have a relatively similar strategy—the production of small numbers of offspring that are fairly large in relation to size of the mother \( (\text{birth length} >25\% L_{\text{max}}) \). These young then grow relatively rapidly, increasing 40–80% of the birth length in their first year. However, this category covers a wide group of sharks from the small, coastal Atlantic sharpnose shark to the large, pelagic shortfin mako. Obviously there are some significant differences in the overall life histories of the individual species within this category. The remaining 12 species have evolved similarly successful strategies but have placed emphasis on different life history characteristics.

Very few species, or stocks, have been investigated extensively enough to estimate mortality rates, especially age specific mortality, however it can be assumed that predation on juveniles probably constitutes a major source of overall mortality on the populations. Because viviparous sharks have a limited uterine space available for embryo development, there is an inverse relationship between the number and size of young produced. With the general slow growth and late maturation exhibited by viviparous sharks (see Cailliet et al. 1986 and Cailliet 1990 for a review) such a reproductive strategy results in a direct relationship between stock and recruitment. Thus sharks, as a group, are extremely susceptible to overfishing (Holden 1974, 1977). The increasing exploitation of adult stocks may result in reduced future cohort strength, leading to insufficient recruitment, and eventual collapse of populations. Because of the multispecies nature of the developing shark fishery, management at the group level will be desirable but difficult to achieve owing to the variations in the life history strategies employed by the different species (Branstetter and McEachran 1986b).

**Acknowledgments**

The Marine Research Institute of the Florida Department of Natural Resources provided facilities for the completion of the manuscript materials.
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